

4.—Animal and plant speciation studies in Western Australia

By H. E. Paterson¹ and S. H. James²

Abstract

Speciation studies involving Western Australian, and especially southwestern, animals and plants are reviewed. The paper presents different approaches to the problems of integrating cytogenetics, ecology and taxonomy, and falls into two parts.

Current studies on animals in Western Australia illustrate some of the consequences of the evolutionary process of speciation, as well as some aspects of the mechanism bringing it about.

Cytocoevolutionary responses in ten groups in the Western Australian flora are reviewed. Cytogenetic innovations in evidence include polyploidy, apomixis, complex hybridity, aneuploidy, lethal systems and B chromosomes, and in general, these are interpreted as conservative devices, conserving either heterozygosity, adapted gene combinations, or both.

These studies support Mayr's arguments for a discipline covering the speciation process and its consequences.

Introduction

Speciation studies amongst Western Australian animals and plants are not extensive, but they illustrate differing points of view in a number of areas. Firstly, the application of a species definition to taxonomic practices varies between zoologists and botanists; for example, the existence of infraspecific polyploidy in plant species must often, perhaps invariably, combine genetically distinct though morphologically similar biological species into a single taxonomic species. Comparable genetic barriers in animal species would normally be taken to delimit taxonomic species. Secondly, there is a continuing discussion concerning the importance of postmating isolation and its reinforcement in the speciation process. In this paper, the theory of allopatric speciation involving an initial attainment of premating isolation is vigorously, and profitably, applied to animal speciation studies. On the other hand, while recognizing that the theory of allopatric speciation may well be of great utility in interpreting the evolutionary origin of many plant species, the plant speciation studies reviewed here have been selected, and in many cases the work actually directed, with a view to seeking out situations in which alternative processes of speciation may be demonstrable. Thus, these latter studies do not concentrate on an integration of genetically-determined ecological attributes with geohistorical circumstances, but attempt to investigate situations where endophenotypic attributes, the attributes of which postmating isolation is made, are of adaptive utility at the infraspecific level.

¹Zoology Department, University of Western Australia, Nedlands, W.A.

²Botany Department, University of Western Australia, Nedlands, W.A.

Animal species studies

by H. E. Paterson

The species concept

In 1957 Ernst Mayr proposed that a Science of Species could be justified as a legitimate field of study. It was conceived as including not only the study of the process of speciation itself, but the study of many of its sequelae as well. Such a field of study would clearly be most closely related to population genetics because it is based on the genetical concept of the species, which, in turn, has the idea of a species-specific gene pool at its centre. The studies reported on here are mostly still in progress. They are diverse in approach and cover a wide range of animal species, but they all fall within the scope of Mayr's Science of Species. By presenting them together it is hoped that they will provide support for Mayr's suggestion by revealing something of the breadth, interest and even utility of such a discipline.

At the outset it is necessary to outline clearly what is meant by the genetical concept of the species, because the species in genetics does not always correspond to any species currently recognised in taxonomy. This usually means that insufficient time has elapsed for the necessary adjustments to be made. A gene pool can only exist in organisms which reproduce sexually, though it could be argued that it is applicable to certain prokaryotic organisms characterised by at least one of Haldane's "alternatives to sex" which would enable recombination to occur (Haldane, 1955; Sanderson, 1971). In sexually reproducing organisms all reproductively mature members of a species can contribute to, and share in its gene pool. Furthermore, the gene pool of this species is isolated from the gene pools of other species due to the functioning of genetically determined isolating mechanisms. For these reasons the gene pool of a species is able to be distinct in genetical properties and structure from those of all other species.

These ideas can be expressed in other ways. For example, the essential characteristic of an animal species is that it comprises a number of individuals each of which is able to recognise reproductively mature mating partners of the same species. This is achieved by means of a genetically-determined, co-adapted behavioural signalling system. Members of a particular species, because of this system, do not usually respond effectively to the analogous signals of members of other species under natural conditions.

The explosive diversification of forms of organisms which apparently followed the evolution of eukaryotic cells in late Precambrian times cannot be attributed to the newly evolved methods of generating genetic diversity alone. Recombination will generate variation, but will not on its own lead to the radiation of forms which we observe. Radiation will, however, be initiated if recombination is restricted to occurring within discrete gene pools. This raises the key question how did the species as an evolutionary phenomenon first arise? No general answer to this question will be attempted because it is very likely that species arose on several independent occasions following the independent acquisition of sexual reproduction by several different eukaryotic Protista (Margulis, 1970). In the following discussion only the animal lineage will be considered. Most animals are dioecious or can be shown to have had dioecious ancestors. This suggests that the whole animal kingdom evolved from an early dioecious protistan ancestor. Because we are discussing the origin of the species as an evolutionary phenomenon, such an ancestral form must have lacked an isolating mechanism as such. However, being dioecious it must have had a genetically-determined mechanism which enabled the one mating type to recognise the other. Credibly, this system could have provided the basis for the first isolating mechanism which brought the first two animal species into existence, because the principles of allopatric speciation long advocated by Mayr (1942; 1963) are as applicable to this basic system as to more advanced ones. In simple terms the mechanism behind allopatric speciation may be as follows. Once an extrinsic barrier has split the original "gene pool" into two, the genetic structure of each will begin to deviate in response to selection from its distinct environment. Some of the gene substitutions brought about in this way will have a pleiotropic effect on the mate selection mechanism. In this way the mechanisms of the two populations will progressively diverge to the point when the signals of members of the one population are no longer effectively recognised by members of the other. At this stage speciation will have been achieved. An example of a gene with pleiotropic effects of the sort invoked is *yellow* in *Drosophila melanogaster* Meigen. When compared with "wild type" flies homozygotes for this allele are more resistant to starvation (Kalmus, 1941) and the males have a modified courtship pattern (Bastock 1956). Following effective long term isolation, the mate recognition systems of the two sub-populations may, thus, also function as premating isolating mechanisms, which effectively protect the integrity of their gene pools. This in turn enables the two populations to continue to diverge adaptively even though their ranges may come to overlap.

Details of the speciation scheme outlined above will be disputed by some, but if it happens to be correct it will be noted to have the following implications. Species come into existence as by-products of adaptive evolution. They are

not products of selection for diversity, though selection may decide whether a newly evolved species will survive for long. Diversity is not selected for as such, and it is ultimately dependent on factors which favour speciation. However, selection does decide the specific pattern of diversity which comes into existence in a particular environment at a particular time.

In Western Australia the work of A. R. Main and his students on Leptodactylid frogs is the pioneer work on animal species studies. This work is still continuing and has recently been reviewed (Main, 1970), which provides an indication of how young a field this is within this State.

Studies on the origin of species

The term "speciation studies" is often used loosely to mean almost any type of species study. Here it is used in a stricter sense to mean the study of the mechanism by which isolating mechanisms, which protect the gene pool of a species from introgression, come into existence.

Earlier work (Main, Lee and Littlejohn, 1958) showed a rich frog fauna in southwestern Australia, an area almost free of geographical barriers of the kind which have proved important in initiating speciation. These authors compared the faunae of southwestern and southeastern Australia, using as particular criteria male call structure and genetic divergence as judged from the results of *in vitro* crosses. They concluded that during the Pleistocene three distinct pluvial periods, separated by interpluvials, had allowed the entry into Western Australia of faunal elements from the east. The arid interpluvial periods effectively led to the splitting of populations into western and eastern sub-populations, thus providing the conditions for subspeciation and speciation to occur. Main (1970) has modified details of the original model, suggesting that the last Pleistocene pluvial, and one of the two earlier connections, were only wet enough to allow frogs from seasonally arid environments to invade from the east. During the third pluvial, however, both wetland and semi-arid country frogs were able to penetrate westwards. This modified model accounts for why there is only one western species representing certain eastern wetland (Bassian) species, while numbers of eastern semi-arid (Eyrean) species each have three western representative species. These ideas have proved applicable to spiders of the tribe Aganippini (Main, 1962), horseflies (Tabanidae) (Mackerras, 1962) and, if allowance is made for the biological features of the group, to birds (Serventy and Whittell, 1951).

The genus *Calliphora* (Diptera) has radiated enormously within Australia, so much so that most of the world's species are endemic here. These flies offer excellent opportunities for testing Main's ideas on speciation at a new level of sophistication. Most species are easily cultured, and pre- and postmating isolation between members of western and corresponding eastern populations can be studied with considerable precision. The eastern and western populations can also be compared with great precision at the cytological level because these flies possess

excellent polytene chromosomes (Thomson, 1969). Their large size make them very suitable for biochemical studies using gel electrophoresis, for example. Such a study is at present in progress. N. Monzu is exploiting some of the techniques mentioned to compare Western Australian species with close relatives in eastern Australia (Table 1).

Table 1

Western Australian species of the genus Calliphora with closely related species in the eastern states of Australia

Western form	Eastern form
<i>Calliphora nociva</i> Hardy <i>Calliphora albifrontalis</i> Malloch <i>Calliphora varifrons</i> Malloch	<i>Calliphora augur</i> (F.) <i>Calliphora stygia</i> (F.) <i>Calliphora hilli</i> Patton

R. W. George* has in recent years paid attention to the rather neglected field of speciation in the sea (George and Main, 1967; George, 1969). The organisms with which he has worked are the rock lobsters, Palynuridae. By considering and taking into account the biological properties of present day species of the genus *Jasus*, for example, he was able to propose credible models of speciation in the sea, which do no violence to the well-accepted ideas of how speciation occurs on land. In this case speciation of a group of six contemporary species which occur in the waters of the southern hemisphere was explained in the following broad terms: George accepts that their close similarity implies a common ancestral species which formerly had a circumpolar distribution. Because global temperatures were formerly higher on the average than now, the ancestral species was thought to have occupied an area occupied by the subantarctic zone today. With climatic cooling this temperate zone must have moved to lower latitudes, forcing the species northwards until it could colonize appropriate regions of the southern continents and several islands (New Zealand, Tristan da Cunha, St. Paul's Island and Juan Fernandez). In this way the original single circumpolar species was effectively fragmented into isolated populations, each of which would then have been subjected to a different set of selection pressures. The isolation could have been maintained by specific local conditions resulting from local currents due to the configuration and position of the island or continent with respect to the prevailing major currents.

In a comparable way speciation in other genera was accounted for. In general, a study of the biological attributes of present day species was considered to provide the key to elucidating the pattern of speciation proposed for each genus.

Earlier work by Littlejohn and Main and his students on the isolating mechanisms operating to maintain the integrity of the gene pools of the frogs *Crinia insignifera* Moore and *C. pseud-*

insignifera Main has been repeated in considerable detail by M. Bull. These two species meet along the Darling Scarp. *C. insignifera* occupies the coastal plain and *C. pseudinsignifera* extends over large areas of the interior of southwestern Australia. Bull has demonstrated clearly that post-mating isolating mechanisms between these species are absent as judged by the *in vitro* cross method. Reproductive isolation between them is therefore largely at the premating level. In transects across the rather sharp line of contact between the species no indication of reinforcement of the premating mechanisms, such as the male calling characteristics, has been revealed. It seems that in this case the premating isolating mechanisms did not come into existence through natural selection acting to reduce gene flow between two partially diverged populations as postulated by Wallace, Fisher and Dobzhansky, among others.

The study of isolating mechanisms

It is generally accepted that postmating isolating mechanisms arise as pleiotropic by-products of adaptive evolution in isolated populations. This is because it is not easy to see how they could be evolved directly by natural selection. Less agreement exists over the origin of premating isolating mechanisms, because less difficulty exists in proposing models which account for their evolution by selection acting against inferior hybrids, as an alternative to their production in the same manner as postmating mechanisms. Many cases of "reinforcement" of premating isolating mechanisms have been reported (Levins, 1970), but it should be appreciated that the mere demonstration that selection strengthens premating isolation can in no way be regarded as compelling evidence in support of the thesis that premating isolating mechanisms evolve in this manner. This is because no satisfactory mechanism has been proposed to explain how genes, selected at a parapatric interface between two populations for their property of reinforcing premating isolation, can spread through the body of each population outside the zone of contact. Because premating isolating mechanisms are properties of species as a whole, models of speciation must account for this fact. This is an old objection (Moore, 1957) but one which is still avoided by many advocates of the hypothesis of the selective origin of premating isolating mechanisms.

S. J. Miles, R. Irving-Bell and I are particularly interested in reproductive isolation between the four members of the *Culex pipiens* L. complex which occur in Western Australia, *C. fatigans* Wd., *C. molestus* Forskål, *C. australicus* Dobr. & Drumm. and *C. globocoxitus* Dobr. here treated as distinct biological species. *C. australicus* has not yet been cultured successfully, but the other three species are readily cultured and can be crossed in the laboratory. Except in the crosses between *C. globocoxitus* and *C. fatigans*, there is little evidence of postmating isolation between them. In cages the premating isolation is detectable but is by no means complete. Yet in nature very little hybridization

*Western Australian Museum.

has been detected, and then only between *C. molestus* and *C. fatigans*, which often share the same breeding place. This is of interest because *C. molestus* was introduced from Europe, *C. fatigans* was introduced, possibly from the oriental region where it almost certainly originated, while the remaining two species are confined to the Australasian region. Thus *C. molestus* and *C. fatigans* do not naturally coexist with each other, or with the two endemic species. Yet they are all very effectively reproductively isolated when brought into coexistence due to man's interference.

Yvonne Henderson is applying the pioneering studies of Margaret Bastock, Aubrey Manning and Herman Spieth to a comparative study of the courtship behaviour of members of the *Drosophila melanogaster* species sub-group, recently reviewed by Bock and Wheeler (Bock and Wheeler, 1972).

N. Monzu's studies of the genus *Calliphora* include the measurement of reproductive isolation between sympatric and allopatric forms. Studies of pre- and postmating isolation between isolated demes of the frog species, *Crinia insignifera*, Moore, by J. Blackwell, have failed to substantiate the suspected existence of a deviation between demes breeding on sand and demes breeding on clay (Main, 1970).

An aspect of the study of isolating mechanisms is the detection of unsuspected sibling species. Using the methods of polytene chromosome cytology C. A. Green has been investigating the taxon *Anopheles annulipes* Walker which has a wide distribution within Australia and its neighbouring islands. Thus far he has detected four sibling species which he has temporarily designated as Species A, B, C and D. The species are readily identified by their X-chromosomes, which have been involved in extensive rearrangement during the course of evolution. Species A and B are sympatric over considerable areas of Western Australia (at least between Kalbarri and Geraldton). Species A and species C co-exist in Southern Queensland. Species D extends southwards from the Ord River possibly as far as Geraldton, though the southern record requires confirmation by means of crossing experiments with an Ord River stock. So far no hybrids have been detected in nature. Studies in this complex are hampered by the need to maintain them in culture by means of artificial mating methods. Crosses are performed in the same way.

Julian Ford and S. A. Parker have recently shown that the Australian Wedgebill comprises two sibling species *Psophodes cristatus* (Gould) in the east, and *P. occidentalis* (Matthews) in the west. The ranges of these two bird species overlap in the region of Oodnadatta, South Australia. The fact that the two gene pools exist was revealed by the use of song analysis (Ford and Parker, 1973).

R. J. Mahon has made use of the gel electrophoresis of heart muscle enzymes to demonstrate that the common blue and orange rock crabs, hitherto referred to as *Leptograpsus variegatus*

(F), actually belong to two distinct species. Until this demonstration *L. variegatus* has been generally regarded as a single polymorphic species.

The study of the genetic structure of species

The study of the genetic structure of species poses particular problems which have been considerably alleviated in recent years with the introduction of gel electrophoresis as a tool with which to score populations for variation at loci determining certain enzymes and other proteins.

Crinia insignifera Moore is a very small Leptodactylid frog found on the coastal plain of south-west Western Australia. The species is broken up into a large number of unusually discrete demes each occurring near a winter breeding site. Because of the small size of these frogs their vagility is considered to be rather low. This situation has been exploited by J. Blackwell to study genetic divergence between demes within a species. Here again use has been made of gel electrophoresis to study variation at loci determining enzymes. Using eight enzyme systems she will have data on at least 10 loci. This information will enable her to study the divergence of demes, and to estimate how effectively each population is isolated from its nearest neighbours. To facilitate the scoring of the gels she has studied the genetics of each system utilized. Studies such as this are much needed as checks on population genetic theory, which has moved well ahead of the studies which are actually feasible.

J. den Hollander is studying the structure of populations of *Musca domestica* L. using loci involved in determining maleness, and by studying variation involving the sex chromosomes. Most Australian housefly populations are characterized by the absence of a Y-chromosome, in sharp contrast to most populations of the species which have been studied elsewhere (Rubini, 1964; Milani, 1964). By using marked chromosomes den Hollander has shown that in the Western Australian flies so far examined there is a male-determining locus only on chromosome III. This is in contrast with Wagoner's (1969) report on a strain from Brisbane which carried male-determining loci on chromosomes II, III and V, and one from Canberra which showed holandric inheritance of a chromosome II (Kerr, 1961). The strain from Canberra was XY in the males and XX in the females, but Wagoner's Brisbane strain was XX in both sexes. In this study den Hollander has only found strains without a Y-chromosome: these stocks came from Sydney, Canberra, Melbourne, Adelaide, Perth, Albany, Kalgoorlie and Kununurra. The results presented in Table 2 have been obtained from crosses between the Perth stock with the others mentioned. Controls and stocks maintain a sex ratio very close to 1.

With further elaboration it is hoped that methods will be developed with which populations of *Musca domestica* from anywhere in the world can be characterized.

Table 2

Sex ratios of crosses between various stocks of *Musca domestica*

Cross	♂ off-spring	♀ off-spring
Perth ♀♀ x Canberra ♂♂	510	115
Canberra ♀♀ x Perth ♂♂	262	229
Perth ♀♀ x Melbourne ♂♂	420	31
Melbourne ♀♀ x Perth ♂♂	553	503
Perth ♀♀ x Ord ♂♂	668	322
Ord ♀♀ x Perth ♂♂	362	388
Melbourne ♀♀ x Canberra ♂♂	659	713
Canberra ♀♀ x Melbourne ♂♂	296	292

Ecological studies

Darwin pointed out that the ecological interactions of closely related species are of particular importance in understanding evolution. For this reason the studies, discussed above, which deal with the *Culex pipiens* complex, the species of the genus *Calliphora* and the crabs of the genus *Leptograpsus*, are all concerned with this subject.

In the *Culex pipiens* complex there are quite marked differences between the four West Australian species. The two native species are not closely associated with man. They breed in natural pools, usually low in organic content, and they rarely feed on man. *C. australicus* will not breed in cages, no doubt because of its ecological requirements for mating-swarm formation. *C. globocoxitus* will mate in small cages and, therefore, it is very probable that its requirements for swarm formation in nature are quite distinct from those of *C. australicus*. This contrast in mating behaviour between the two sympatric endemic Australian species is reminiscent of the differences between the two endemic members of the complex in Europe, *C. pipiens*, which resembles *C. australicus* in requirements and *C. molestus* which is comparable with *C. globocoxitus*. *C. australicus* has been recorded as feeding on rabbits and birds (Lee *et al.*, 1954). Neither endemic species appears to bite man in nature. *C. fatigans* and *C. molestus* both bite man and poultry. The latter species can survive without blood meals (i.e. it is autogenous) since females in their first gonotrophic can ripen their ovaries on reserves laid down during the larval stages. Autogeny has a relatively simple genetic basis, but nevertheless, it has a striking effect on the ecology of the species by freeing it from dependence on vertebrate hosts. This enables it to penetrate the far north of Europe by invading sheltered underground cellars, underground railway tunnels, etc., provided breeding places are available, and despite the fact that it cannot hibernate. This in turn might be expected to lead to a greater degree of inbreeding than is found in the anautogenous members of the complex. These ecological topics are being explored by R. Irving-Bell.

N. Monzu's study of blowflies of the genus *Calliphora* includes an attempt at defining the niche of each common carcass-breeding species. Much work has been done on blowfly ecology, but most of it has been done in the laboratory and relatively little in the field. Yet studies on interspecific competition, for example, are only realistic if they take into account such factors as the behaviour patterns which determine choice of oviposition site and the seasonal peaks of abundance of the species. Other factors to be considered are adaptations such as ovoviviparity and fecundity, the behaviour of larvae in relation to parasites and predators, geographical distribution and interactions with exotic blowflies which have intruded into the Australian scene.

The sibling species of the rock crab genus *Leptograpsus* show slight but palpable ecological differences which were first detected by Shield (1956), but recently studied in greater detail by Mahon. The blue species is more resistant to desiccation than is the orange, and as a consequence it can move and feed at a greater distance from the splash zone to which the orange species is more or less limited. The two species show slight differences in breeding season as judged by the numbers of females carrying eggs attached to pleopods on their abdomens, differences in habitat preference as shown by clumping in transects along the reefs, and in geographical distribution.

The role of symbiosis in the *Culex pipiens* complex of mosquitoes

Early workers on the *Culex pipiens* complex found that crosses between certain colonies of *Culex molestus* from various parts of Europe were incompatible in one or both directions (Marshall and Staley, 1937). This phenomenon was later studied in detail by Laven (1953) who demonstrated that the incompatibility involved mosquito genotypes and cytoplasmic "factors". This has suggested to several authors (e.g., Rai, 1967 and Irving-Bell and myself), that the factors may in fact be symbiotic microorganisms analogous to the sigma factors in *Drosophila melanogaster* (L'Heritier, 1970). This idea has been resisted by Laven (e.g., 1967). He has considered the factors to be RNA (Laven, 1967) and more recently his colleague Jost has suggested that they are DNA particles (Jost, 1970). However, Laven's basis for rejecting the symbiont hypothesis does not appear very impressive. The early work of Hertig & Wolbach (1924) and Hertig (1936) suggested to Yen and Barr (1971) and independently, to Irving-Bell and myself (Irving-Bell & Paterson, 1973) the hypothesis that the cytoplasmic factors of Laven are rickettsiae. Yen and Barr and we have confirmed the work of various earlier workers (Hertig, 1935; de Zulueta, 1964 and Byers & Wilkes, 1970) by detecting rickettsia-like symbionts in the ovaries of members of the complex. The species in which they have been found by us are *Culex molestus* and *C. fatigans* from Australia and *C. pipiens pipiens* L. from England. We have failed to find them in the

endemic Australian species, *C. globocoxitus* and *C. australicus*, but have detected virus-like particles in their place in these two species.

Our attempts at relating the micro-organisms to the phenomenon of cytoplasmic incompatibility have been held up by our inability to detect incompatible populations in *C. fatigans* or *C. molestus* in Australia, despite their reported existence (Dobrotworsky, 1955). However, Irving-Bell has recognised in *C. fatigans* and *C. molestus*, an apparently new form of degeneration in the oocytes which is distinct from that found with natural abortion. This type of degeneration coincides with a large increase in the numbers of symbionts, and she is now investigating the connection between the two phenomena. The symbiotic relations which have been described above are evidently of long standing, since the one appears to be older than the species *C. pipiens*, *C. fatigans* and *C. molestus*, and the other evidently predates the divergence of *C. globocoxitus* and *C. australicus*. Experiments now in progress are investigating whether the two types of symbiont can be obtained in the same cytoplasm, and the interaction of the various genotypes with the various symbionts.

Concluding remarks

The studies reported on here will give some impression of the scope of Species Studies as defined above. All the studies mentioned were designed from a purely scientific point of view, but it will be noted that those involving pest animals are of considerable practical value as well. All are essentially studies of single species. In other words, they are studies at the population level of complexity. Species Studies are also an essential first stage in the study of ecosystems. This is, of course because the organisation which is apparent at the community level results from selection acting at the level of the individual within a species. The ecosystem comprises a physical environment occupied by a number of species. Ultimately its structure depends on the process of speciation although, more immediately, it may depend on the migration of species. In turn, the coadjutment of a migrant species and the ecosystem provides the selective pressure which lead to speciation under the system outlined in the introduction to this section of the paper.

The significance of Species Studies might seem obvious, and yet they are rarely pursued in the way which Mayr had in mind. That much remains to be done is shown by the fact that disagreement is still widespread over so fundamental a matter as the process of speciation. We find population biologists of high standing quite unable to agree on the answer to a question such as: "Are species the product of direct selection for diversity, or are they by-products of adaptive evolution?". And yet each alternative carries with it far reaching and contrasting evolutionary implications.

Cytogenetic aspects of the speciation process in plants

by S. H. James

Perspective

The more characteristic elements of the Australian flora have been investigated cytologically, mainly by Smith-White, and his findings and those of other cytologists have been integrated with a geological history of the continent to produce a rather satisfying, yet suggestive, picture of the evolution of our flora. In summary, the hypothesis developed is as follows (Smith-White, 1959). The angiosperms originated elsewhere than in Australia. Before their entry into Australia they achieved geographical expansion over the major continents and underwent adaptive diversification. The major orders and families were established whilst the Australian continent remained geographically isolated and unavailable. Isolation of Australia was temporarily broken down during the middle Cretaceous, and a massive angiosperm invasion occurred, leading to the replacement of the older more primitive flora. The invading angiosperms included only those lineages which were near the "bridgeheads". Subsequent isolation of the continent has allowed the immigrant flora to indulge in a second evolutionary cycle which has resulted in the establishment of the present day autochthonous groups. These groups (e.g. Boronieae of the Rutaceae, Chamaelaucoideae-Myrtaceae, Proteoideae and Grevillioideae-Proteaceae, and the Section Cryptostomae of *Casuarina*-Casuarinaceae) show remarkable variation in chromosome number; they contain considerably more gross cytological variation than their extra-Australian relatives. Generally, this variation is shown by differences between the chromosome numbers characterizing genera, but within the genera the numbers are constant. The diversity in generic chromosome numbers originated during the early phase of the Australian evolutionary cycle, just as the diversity in numbers between orders and families developed in the earlier extra-Australian primary radiation, and in a pan-Australian flora. Dissection of this pan-Australian flora into its eastern and western components occurred in the Miocene, after the establishment of present day genera, and this dissection, established first by marine intrusion, has been maintained by the Great Australian Desert (Crocker and Wood, 1947), and progressive evolution within these isolates has led to the development of their own suites of species within common genera. Continentally, recent phytogeographical events include a partial breakdown in isolation allowing the entry of modern Indo-Malayan elements; changes of climate and topography, particularly the relatively recent (Quaternary) establishment of alpine conditions in Eastern Australia, which has allowed the establishment by long distance dispersal and by intrusion from the north along the montane tableland route of a "Southern" element showing affinities with New Zealand and South America; and a general

contraction, in Western Australia, of the autochthonous elements to the south west corner, associated with a general increase in aridity (Crocker, 1959; Churchill, 1961).

The recent immigrants, especially the herbaceous ones, are of particular interest. They may be expected to show, and do show, a third order cycle of adaptive diversification. By studying the distribution of cytogeographical races and their genetic systems, it should be possible to gain information which, in time, may contribute to a coherent picture of the dynamic phytogeography of the Quaternary. Significant work in this field, for mainly eastern taxa, has been done by Hayman (1960), Briggs (1962) and Peacock (1962).

In his essay on the cytological evolution in the Australian flora, Smith-White (1959) developed an hypothesis to account for the chromosome number variation discussed. He suggested that adaptive diversification of the original immigrant lineages was mediated by a multiplicity of newly available habitats, and by reduced biological competition. Consequently, the immigrant flora underwent an evolutionary cycle which "favoured genetic experiments, including experiments in structural changes and in chromosome number". This hypothesis implies that the changes in chromosome structure and number involved are basically innovative in nature. On the other hand, it is frequently argued (Darlington, 1958; Lewis and John, 1963) that such changes find their adaptive utility as conservative devices.

Much of the current cytological research on the Western Australian flora, reviewed below, is directed towards an understanding of the genetic systems operating in particular, mainly herbaceous, plant groups to determine how, and with what consequences, these groups have responded to the vicissitudes of a new environment. A major aim is to evaluate the role of chromosome changes as innovative and conservative devices, and to determine whether in fact, particular types of genetic architectures, at the population level, are associated with particular types of cyto-evolutionary responses. In this way, it may be possible to account for the cytological diversity characterising the endemic Australian tribes.

Calcectasia cyanea—ancient and unchanging

Green (1964) has listed the species which occur in both Eastern and Western Australia. Of these, many are equipped with small seeds or other such devices that might allow for long distance dispersal. A few species showing this disjunct distributional pattern, however, are not so equipped, and their occurrence poses an important problem. What is the basis of their conservatism? Anyway (1969) investigated the variation pattern and genetic system of *Calcectasia cyanea* R.Br., the blue tinsel lily, and noted there to be little morphological and phytochemical variation between populations within its distributional range. However, the difference in habit exhibited between the extensively rhizo-

matous plants of the eastern populations and the shortly rhizomed plants of Western Australia was taken as a key character in differentiating these taxa at varietal rank. The general exophenotypic constancy, however, was shown to be associated with a conservative genetic system in which Anyway was able to demonstrate a close relationship between the frequency of chiasma formation in the long arm of chromosome no. 9, which constitutes some 20% of the total genetic material, and the percentage frequency of sterile pollen. It appears that all *C. cyanea* plants are self pollinating and heterozygous for differentiated chromosome 9 long arms, and that recombination between these "supergenes" results in the synthesis of gene combinations lethal in the haploid phase. As Anyway concludes: "The lack of .. (genetic) .. flexibility has prevented significant evolutionary change, and the species is now restricted to those limited areas which provide the ecology to which it is adjusted. *Calcectasia* is a true relic, apparently committed to ultimate extinction by the adoption of an ultra-conservative genetic system."

Isotoma petraea—recent complex hybridity

Isotoma petraea F. Muell. is another species which has evolved a system of permanent hybridity. It is a largely autogamic species which occurs in discrete populations on granite outcrops and other rocky areas throughout the Ereman Province of Australia. In the southwestern corner of its distributional range in Western Australia, complex hybridity has evolved; the populations are made up of plants heterozygous for multiple interchanges, made permanent by the operation of its autogamic breeding habit and a system of balanced lethal genes. A detailed hypothesis concerning the evolutionary origin of this genetic system from structurally homozygous progenitors has been developed (James, 1965; 1971).

Beltran (1971) has investigated the generation of hybrid vigour in interpopulational crosses in *I. petraea*. He has shown that the degree of heterosis achieved in such crosses depends in large measure upon the genetic systems of the parents involved. Intropopulational hybrids between structural homozygotes will show substantial heterosis if the parental populations exhibit little outcrossing, and little or no heterosis if the parental populations exhibit substantial amounts of outcrossing. Intropopulational hybrids between complex heterozygotes exhibit either no or negative heterosis. These results suggest that the *I. petraea* population system may be viewed as a series of lineages inbred to varying degrees; amongst the structural homozygotes, crossing generates heterosis, the degree and significance of which depending upon the relative degree of inbreeding characterising the parents, but all the structurally homozygous populations constitute a single coadapted gene pool in that the union of gametes drawn from different populations produces a hybrid as vigorous as or more vigorous than the

parents. On the other hand, amongst the complex hybrid populations, the absence of heterosis in interpopulation hybrids conforms with the hypothesis that the complex hybrids are already conserving high levels of genetic hybridity, and the negative heterosis observed in some inter-population hybrids suggests that coadaptation no longer exists between the complex hybrid populations.

Laxmannia—responses to autogamy

Laxmannia, a member of the tribe Johnsonieae of the Liliaceae is one genus which promises rewards for detailed biosystematic studies (Keighery, unpublished). Possibly the most striking morphological feature in this genus is the development of shortly to strongly pedunculate inflorescences in most species, with sessile inflorescences in *L. sessiliflora* Dene. This suggests that natural selection has favoured a more effective presentation of flowers and, therefore, cross pollination. More importantly, *L. sessiliflora* has an open pollinating mechanism while the rest of the species so far examined have a floral mechanism in which open flowers are presented for cross pollination, but closure of the flowers in the evenings causes the anthers, still with pollen attached, to be pressed on to the stigma, to effect self pollination. However, a comparison of seed set following selfs and crosses shows that the products of self pollination in these latter species are to a large extent eliminated by lethals operating post zygotically. This seems to be a rather inefficient system, involving the wastage of many ovules, a situation particularly important in *Laxmannia* where, it is interesting to note, the number of ovules per flower is three in *L. sessiliflora* and increases to 15 to 21 in species with lethal systems. Additionally, in *L. ramosa* Lindl., certain populations on the coastal plain around Perth exhibit high frequencies of interchange heterozygotes as well as the automatic self-pollination system and the elimination of selfed products by lethal systems. Again, there is a conjunction of interchange exploitation and the generation of lethal systems in association with a change in the breeding system towards autogamy, but the system has not achieved the rigidity of that exhibited by *Isotoma petraea*. *Laxmannia squarrosa* Lindl. is a highly variable species, and with *L. grandiflora* Lindl., *L. sessilis* Lindl. and several other forms, constitutes a complex of some taxonomic confusion. These species exhibit the automatic self-pollination mechanism described above, post-zygotic elimination of selfed products, and a variety of other cytogenetic devices including chiasma localization, polyploidy, aneuploid reduction, and a complex but as yet unresolved pattern of genetic coadaptation between forms. It is clear that an understanding of the genetic architecture and strategies of this group will greatly facilitate the construction of a meaningful taxonomy.

Stylidium—lethals and aneuploidy

Stylidium is one of the more remarkable components of the Western Australian flora. It is by far the largest genus of the Stylidiaceae, a family restricted to Australia (including Tasmania), New Zealand and Antarctic South America, plus a few species penetrating back into the Indo-Malayan region. Of the 140 species currently recognized, 102 occur in the south-west of Western Australia, 30 occur in northern Australia and beyond, while 8 occur only in the eastern states. A comparison of the cytological information presently available indicates that the base chromosome number is $x = 15$, a number constant, except for polyploidy, amongst all the eastern states and New Zealand records. However, associated with the radiation of species that has occurred in the south-west of Western Australia, is a massive propensity for aneuploid reduction. In Western Australia, chromosome numbers ranging from $n = 16$ down to $n = 5$ have been recorded, with polyploidy occurring on 15, 14 and 13 (James, 1973; Banyard, 1973). Aneuploid reduction series are in evidence in most sections of the genus as recognised by Mildbraed (1908), with possibly several independent reduction series occurring in some of the larger sections. Carlquist (1968) has commented upon the bio-systematic interest of the Stylidiaceae and upon the lack of published information. He speculated upon the factors which may have contributed to its striking speciation in Western Australia, and suggested that adaptation to pollination vectors and to soil mosaic patterns may have been of prime importance. The information on chromosome number variation, which was not available to Carlquist, is indicative, however, of important cytogenetic situations.

The genetic systems and biosystematic relationships in several species groups in *Stylidium* have been investigated. Farrell (1973) has shown that *Stylidium calcaratum* R.Br. and *S. ecorne*,* the latter formerly considered to be a variety of the first, differ in chromosome number ($n = 11$ and $n = 13$ respectively). *S. ecorne* having the higher number, may be considered primitive to *S. calcaratum*, and this directional reading of the evolutionary sequence conforms with the proposition that the well developed floral spur and the adaptation to more xeric habitats characteristic of *S. calcaratum* are derived conditions. Seed set following selfing in both species is as good as that following intrapopulation crosses. However, interpopulation crosses in *S. ecorne* yield high seed sets, but in *S. calcaratum* reduced seed sets, relative to intrapopulation crosses, are found. Thus, the evolution of *S. calcaratum* from *S. ecorne*-like ancestors has involved not only the acquisition of a perfected floral spur and an increased ecological amplitude, but also an aneuploid reduction of chromosome number, and a loss of coadaptation between the *calcaratum* populations.

**S. ecorne* is a manuscript name to be formally published in Farrell (1973), the taxon so named is equivalent to *Stylidium calcaratum* var. *ecorne* F. Muell. ex Erickson and Willis.

Banyard (1973) has made comparable studies on *S. elongatum* Benth. (n 13 and 26), *S. confluens** (n=14) and *S. crassifolium* R.Br. (n 14 and 28), three distinct species considered by Carlquist (1968) to form a continuous variational cline. In all three species, at the diploid level at least, comparison of seed set following selfing and intrapopulation crossing demonstrate the elimination of most selfed products by the operation of post-zygotic lethals. Inter-population crosses show that there is again, in all species, a breakdown in coadaptation. Best seed set is obtained in interpopulation crosses involving parents drawn from populations some 15 to 40 miles apart. When the interparental distance is 100 to 150 miles, the seed set is reduced to levels comparable to that obtained in intrapopulation crosses. Thus, it would seem that in these species, individual plants are heterozygous for several to many recessive lethal genes, and these lethals are shared by most or all members of a population. The arrays of lethals vary from population to population and populations sufficiently distant have fewer lethals in common. However, increasing distance between populations is associated with increasing genetic divergence, and this may be fostered either by exophenotypic adaptation to differing environmental circumstances, or by random, perhaps neutral, endophenotypic variation.

Tetraploid races occur in both *S. elongatum* and *S. crassifolium*. In the latter, the tetraploids occur towards the centre of the species range; the species is characteristically distributed in this region as very small localized populations which must perforce be relatively inbred. Since the ancestral diploid populations contain arrays of recessive lethal genes within their gene pools, it seems certain that the role of tetraploidy here is to conserve hybridity. A similar role may be attributed to tetraploidy in *S. elongatum*, but in this case, the species occurs as small scattered populations in yellow sandplain, in contiguous association with diploid *S. elongatum* to the west and diploid *S. confluens* to the south and east. Thus, it may well be that the adaptive utility of tetraploidy here is found in the genetic barrier it establishes between these three ecologically-differentiated contiguous forms.

Stylidium brunonianum Benth. (n=9) is an extremely variable species. Typically, local populations are made up of one or a few forms differing from each other in various morphological and ecological attributes. Each biotype appears to have its own suite of characteristics. One infraspecific taxon, sub sp. *minor*, seems of valid rank, but within sub sp. *brunonianum* the variation pattern cannot be partitioned into a satisfactory infraspecific taxonomy. The limits and relationships of *S. striatum* Lindl. *S. rigidifolium* Mildbr. and *S. brunonianum* sub sp. *brunonianum* are most confused. Ling (unpublished) and Stone (unpublished) have in-

vestigated the genetic systems found in this group. Again, post-zygotic lethals operate to eliminate the products of self pollination, and inter population crosses reveal a breakdown in genetic coadaptation between populations as in *S. elongatum*, *S. confluens*, *S. crassifolium* and *S. calcaratum*. However, in *S. brunonianum*, the loss of coadaptation with interparental distance is much more rapid than in the other species mentioned; the optimum interparental distance being in the order of miles rather than tens of miles. *S. brunonianum* shows further developments in its genetic system in that many populations exhibit high frequencies of male-sterile plants in which the anthers abort soon after pollen mother cell meiosis, and the stigma develops precociously within unopened buds. In addition a high proportion of the male-fertile plants exhibit substantial degrees of pollen sterility, although no cytological aberrations have been associated with this. In one population examined, Stone (unpublished) found a multimodal distribution of pollen sterilities among plants, with a pronounced peak around the 50-60% sterility level. This suggests the existence of synthetic gametic lethals, in which recombinant products from an independently assorting bifactorial system are lethal.

The extent to which lethal systems have been developed in *Stylidium* appears to be quite novel, if not unique, and it seems safe to predict that causal association between lethal system exploitation and the aneuploid speciation method involved will accumulate in the future. Although the details of the speciation methods operative in this genus have yet to be resolved, it is incontestable that the phenomena reviewed above have anything but profound effects on the biosystematics and evolutionary potentials of the group.

Dampiera linearis—polyploidy and B-chromosomes

Dampiera linearis R.Br. is a species of the Goodeniaceae to which attention was initially drawn by Peacock's (1963) observation of intra-specific polyploidy. Bousfield (1970) has shown that in this species there is a wide-ranging hexaploid race in the southwestern corner of Western Australia, a tetraploid race on the lower western coastal plain and two disjunct areas of diploids, one near Albany, the second confined to the Wicher Range below Busselton. The diploids are cross incompatible with the tetraploids and hexaploids, and all forms exhibit a self-incompatibility system based on an interaction between pollen tubes and stylar tissue. Detailed analyses of the Wicher Range area has shown that the diploids are confined to the elevated lateritic caps of the old land surface, while the tetraploids occur on the alluvial soils of the erosion valleys incising the plateau and on the coastal plains. In addition, the diploid populations on the ecotonal slopes contain many plants with from one to five B chromosomes, indicating yet another cytoevolutionary response. Bousfield has clearly demonstrated B chromosome/A chromosome interactions, including

**S. confluens* is a manuscript name to be formally published in Banyard (1973). The taxon so named is presently embraced in *Stylidium crassifolium* R.Br. subsp. *crassifolium sensu* Carlquist.

physical associations between B's and A's during meiotic prophase, and a polarized nondisjunction of A chromosome bivalents at anaphase-1 which is directed such that the nondisjoining bivalents become associated with nuclei containing high numbers of B chromosomes. A survey of the population concerned showed that plants without B chromosomes were either highly pollen fertile or had substantial pollen sterility, while plants with one or more B chromosomes were never associated with the "substantial" pollen sterility levels. There is, then, a striking lack of substantially pollen-sterile plants with one or more B chromosomes in the population. From this, it is inferred that there are plants which are potentially capable of exhibiting substantial pollen sterility, and these are postulated as "interpopulational hybrids", but which have had their fertility restored by a B chromosome effect, and this effect is postulated as being a system of bivalent co-orientation which reduces the segregational fractionation of the divergent genomes combined in these interpopulational hybrids.

Thus, the biology and the cytogenetics of the situation have been integrated into an evolutionary hypothesis which proposes the following. The primitive diploids on the lateritic caps are unable to penetrate the coastal environment. However, genetic recombination at the diploid level in peripheral ecotonal situations has allowed the construction of genotypes which are better adapted to the novel ecology of the coastal plain, and systems contributing to the conservation of such newly fabricated genetic combinations are subjected, therefore, to strong positive selection pressure. The B chromosome system is the conservative device selected in this case. A consequence of B chromosome activity here, however, is A bivalent nondisjunction in interpopulational hybrids. It is proposed also, that this aberration may lead to the production of totally unreduced gametes and hence provide a mechanism for the origin of polyploids adapted to the coastal plain environment. This interpretation for the evolutionary origin of tetraploidy in *D. linearis* is strengthened by the finding of a single tetraploid plant carrying some six B chromosomes.

Although the interpretations of the observed phenomena are somewhat speculative at this stage, *Dampiera linearis* offers an exquisite opportunity to study in detail the evolutionary process of biological speciation. Present information suggests, then, that the invasion of the coastal plain by the derived tetraploids is not due to an increased ecological amplitude of tetraploidy *per se*, but that tetraploidy provides a mechanism of totally conserving genotypes assembled at the diploid level, the whole process being mediated by the unique properties of the B chromosome system.

Eremophila glabra-polyploidy and ecological preference

In *Eremophila glabra* (R.Br.) Ostenf., Ey and Barlow (1972) have demonstrated a relationship between chromosome number and ecolo-

gical preference. Although their intensive work was centered around the gulfs area in South Australia, the species is widespread in Western Australia. In this group, the diploid progenitors occur as localized populations in temperate refugia. The tetraploids are more widespread, but still relatively restricted compared to the hexaploids, and occur in temperate to semi-arid areas, while the hexaploids are of widespread distribution throughout the arid region. Thus progressive adaptation to the arid environment is associated with increasing euploid levels. Similar patterns of geographical replacement of euploid races in other species of *Eremophila* have been documented by Barlow (1971) on a less detailed scale, with "strong indications that the ancient land surfaces of Western Australia are a reservoir of relic diploid populations of *Eremophila*". Barlow discusses the possible roles of polyploidy in the genus, and suggests that "the conservative genetic effects of polyploidy in reducing segregation in newly arisen, highly adaptive heterozygous outbreeding biotypes are . . . of far greater evolutionary value than its supposed role of restoring fertility to partly sterile hybrids." In this he is in accord with the conclusions reached by Bousfield (1970) concerning the role of polyploidy in *Dampiera linearis*. A similar interpretation of the role of polyploidy is considered by Banyard (1973) concerning the tetraploid race of *Stylidium elongatum*.

Cassia—polyploidy, hybridization and apomixis

In *Cassia* (Caesalpinaceae) the species of the series *Subverrucosae* of the section *Psilorhegma* exhibit a very complicated biosystematic situation. Randell (1970) has extensively surveyed this group throughout the Eremean Province, and although her work was largely concerned with central Australian populations, probably similar situations obtain in Western Australia. The following interpretation was developed. Polyploid forms are widespread throughout the Eremaea. The diploid species are confined to mountain refugia such as the Macdonnell, Flinders and Kimberley Ranges, and are apparently fairly strongly isolated from each other in that no evidence of hybridization at the diploid level has been obtained. However, infraspecific polyploid races occur and interspecific hybridization at the tetraploid level, and between tetraploids and diploids, apparently occurs with considerable frequency, generating taxonomically confusing hybrid swarms containing several chromosome numbers. In addition, facultative pseudogamous adventitious polyembryony occurs in the polyploid forms, leading to a competition between the single sexual and up to nine apomictic embryos within the single embryo sac. There is some evidence that the components necessary to assemble this genetic system, namely mechanisms for generating diploid gametes and inducing adventitious polyembryony, may be found at the diploid level.

Once assembled, this remarkable system provides for many things. Sexual reproduction and hybridization between disparate forms generates

hybrids which may themselves have an adaptive advantage in heterotic vigour, and from which the sexual process may assemble a limitless array of novel genotypes. Any genotype is potentially conservable by the apomictic mechanism, but the pseudogamous and facultative nature of this mechanism requires sexual experimentation to proceed. The products of sexual fertilization are subjected to a competitive screening against adventitious embryos of maternal genotype during seed formation. Thus ovules carrying "inferior quality" sexually produced embryos are not wasted, but instead they carry embryos of an already tested genotype. These *Cassia* population systems seem to have achieved a remarkable balance between innovative sexuality and conservative apomixis.

Other groups—possibilities

Several other groups have been investigated cytotaxonomically, and here interesting situations which may well respond to detailed cytogenetic analysis are in evidence. For example, intra- and interspecific polyploidy have been observed by Brittan (unpublished) during his wide-ranging experimental taxonomic study of the genus *Thysanotus*. Polyploid cytotypes have been found in 13 of the 27 species so far investigated cytologically. There appears to be some correlation between the occurrence of polyploidy and a change in the pollination mechanism towards inbreeding. In some of the polyploid forms the anthers dehisce along their full length by longitudinal slits instead of by terminal pores as is usual in the genus. Under insect-free glasshouse conditions it is found that capsules are regularly developed by non-manipulated flowers as a result of self pollination associated with the freely dehiscing type of anther, whereas capsules only form in the pore dehiscing types when manual self pollination has been carried out. This association of polyploidy and self pollination occurs in *T. patersonii* R.Br., the genus' most widespread species in Australia which exhibits polyploidy at the tetraploid, hexaploid and octoploid levels, in *T. tenuis* Lindl. which is of relatively restricted occurrence and uniformly hexaploid, and in *T. multiflorus* R.Br. Interestingly, in *T. multiflorus*, tetraploids exhibiting pore dehiscence occur as well, and Brittan (1962) has suggested that this form is of amphidiploid origin. It seems that in this genus, further cytogenetic work may be able to discriminate between differing roles for polyploidy, even at an infraspecific level.

Secondly, *Drosera* is well developed in Western Australia, having some 34 species currently recognised. Chromosomally, the genus is quite constant on a base number of $x=10$ except in the section *Lamprolepis*, the pygmy sundews, where aneuploid reduction to $n=5$ has been established (Marchant, unpublished). The pygmy sundews with the lower numbers tend to occur in discrete localized populations whereas the wider ranging species maintain the primitive chromosome number. It will be of interest to learn of any other endophenotypic differences,

as well as exophenotypic differences, which differentiates the section *Lamprolepis* from the rest of *Drosera*.

Similar suggestive observations have been made by Bennett (1972) concerning *Hybanthus*, a shrubby genus of the Violaceae. Here it seems that a primitive aneuploid reduction series, $8 \rightarrow 6 \rightarrow 4$, is represented in present day taxa. In the section *Variables*, the widespread Western Australian taxa, *H. floribundus* (Lindl.) F. Muell. subsp. *floribundas* ($n=6, 12$ and 24), *H. calycinus* (DC. ex Ging.) F. Muell. ($n=6$ and 12) and *H. epacridoides* (C. A. Gardn.) Melch. ($n=12$) include polyploid cytotypes, while four diploid taxa have restricted distributions. This pattern is somewhat confounded, however, by the presence of the polyploid *H. bilobus* C. A. Gardn. ($n=12$ and 24) which is of relatively restricted occurrence, and the diploid *H. monopetalus* (Roem. et Schult.) Domin ($n=4$) which is widespread in the eastern states. Bennett (loc. cit) also notes that pollen fertility is characteristically quite high in the widespread *H. floribundus* and *H. calycinus*, and characteristically rather low in the other Western Australian taxa. It would seem again, that different genetic strategies are associated with different degrees of success, and detailed comparative studies on the cytogenetics of *Hybanthus* species may well prove rewarding.

In like manner, comparative cytogenetic studies involving *Verticordia*, *Darwinia* and other members of the Chamaelaucoideae and members of the cytologically invariant Leptospermoideae may indicate a causal basis for the strikingly different cytological responses in these two tribes of the Myrtaceae. Clearly, such an approach can be extended to any group. Indeed, the Western Australian flora provides a formidable store of materials for research into the processes of biological diversification and speciation.

Concluding remarks

Isotoma, *Laxmannia* and *Stylidium*, and probably *Calactasia*, exhibit lethal systems which eliminate the relatively homozygous products of self-fertilization. The polyploidy in *Eremophila*, *Cassia*, *Dampiera*, *Stylidium* and *Thysanotus* may be interpreted as a system allowing the maintenance of high levels of hybridity within populations, though other bases for its adaptive utility are possible and even preferred. Nevertheless, it would appear that natural selection has favoured systems that facilitate a pursuit of hybridity during the differentiation of these groups in the semi-arid to arid Western Australian environment. Genetic hybridity is necessary for the construction of new adapted gene arrays by recombination, and the evolutionary success of lineages fostering hybridity may well be achieved through default of the relatively homozygous lineages. On the other hand, heterozygosity *per se* may somehow code for a more efficient, flexible and adaptive phenotype than can homozygosity. The occurrence of heterosis in interpopulational hybrids amongst

naturally occurring structural homozygotes in *Isotoma petraea* and the dependence of the extent of the heterotic effect on the breeding system of the parents suggests value in heterozygosity *per se*. In the *Isotoma* complex hybrids and in *Laxmannia* and *Stylidium* hybridity has been fixed by the lethal systems, and these have led to a marked differentiation between populations resulting in what here has been called a loss in coadaptation. The intrinsic barriers to reproduction so established between populations in *Stylidium* and *Laxmannia* may well provide the beginnings upon which speciation may be built.

The self incompatibility system in *Dampiera linearis* would seem to be a much more efficient and less divisive system of excluding self fertilization products. So far, little work on the extent of self incompatibility systems in the Western Australian flora has been done. Another system which prevents self fertilization is dioecy, and McComb (1968, 1969) has concluded that the evolution of dioecy and polyploidy are independent responses associated with the maintenance of high levels of heterozygosity in *Isotoma fluviatilis* (R.Br.) F. Muell. in New South Wales. McComb (1966) has also analysed the frequencies of the various sex forms in the floras of the South-west Province of Western Australia and of the British Isles, and has compared these with each other and with the analysis of the South Australian flora made by Parsons (1958). It was shown, *inter alia*, that the proportions of species with hermaphrodite flowers in South Australia and Western Australia are comparable to each other (88.9% and 90.0% respectively) and significantly greater than in the British Isles (80.7%). Additionally, it was demonstrated that the average number of species in the Western Australian hermaphrodite genera is 9.4 while in the British Isles hermaphrodite genera it is 2.8. The average number of species per genus for non-hermaphrodite genera shows much less disparity, 4.1 for Western Australia and 3.1 for the British Isles. Thus, the Western Australian flora has proportionately fewer sexually differentiated species and, among the hermaphrodites, significantly larger genera than has the British Isles. These differences may reflect the different states of development of plant systematics in the two regions, or it may reflect biologically important differences. The following speculation is irresistible. The Western Australian flora is younger and evolutionarily more dynamic than that of the British Isles; the adaptive diversification of its components is associated with the exploitation of a variety of devices conserving hybridity or adaptive gene arrays, or both, and some of these conservative mechanisms are more divisive than others. Divisive mechanisms must result in the fragmentation of the gene pool, and in speciation. The resources of genetic variation available within each product species would be relatively restricted compared with that available to the whole. As the Western Australian evolutionary dynamism dissipates, those lineages which adopted the less

restrictive conservative systems may be expected to have the better chances of survival. Lineages which have adopted dioecy to maintain hybridity may fare much better than hermaphrodites encumbered with lethal systems and, through natural selection, the spectrum of sex forms in this flora may eventually approach that of the British Isles.

Acknowledgements.—We sincerely thank our students and colleagues who have permitted us to outline much of their unpublished information and who, through their lively and enthusiastic argument and discussion, and through their own researches, have much influenced our ideas. We are grateful for the support from grants provided by the Australian Research Grants Committee and by the University of Western Australia for research in these fields.

References

- Anway, J. C. (1969).—The evolution and taxonomy of *Calectasia cyanea* R.Br. (Xanthorrhoeaceae) in terms of its present-day variation and cytogenetics. *Australian Journal of Botany* 17: 147-59.
- Banyard, B. J. (1973).—Biosystematics of the *Stylidium crassifolium* group. (In preparation)
- Barlow, B. A. (1971).—Cytogeography of the genus *Eremophila*. *Australian Journal of Botany* 19: 295-310.
- Bastock, M. (1956).—A gene mutation which changes a behaviour pattern. *Evolution* 10: 421-439.
- Beltran, I. C. (1971).—“Embryology, balanced lethal systems and heterosis in *Isotoma petraea*” Ph.D. Thesis, University of Western Australia.
- Bennett, Eleanor, M. (1972).—A revision of the Australian species of *Hybanthus* Jacquin (Violaceae). *Nuytsia* 3: 218-41.
- Bock, I. R. and Wheeler, M. R. (1972).—The *Drosophila melanogaster* species group. *University of Texas Publication* 7213. 1-102.
- Bousfield, L. R. (1970).—“Chromosome races in *Dampiera linearis* R.Br.” Ph.D. Thesis, University of Western Australia.
- Briggs, Barbara G. (1962).—Interspecific hybridization in the *Ranunculus lappaceus* group. *Evolution* 16: 372-90.
- Brittan, N. H. (1962).—Variation, classification and evolution in flowering plants:—with particular reference to *Thysanotus*. *Journal of the Royal Society of Western Australia* 45: 1-11.
- Byers, J. R. and Wilkes, A. (1970).—A rickettsia-like micro-organism in *Dahlbominus fuscipennis* (Zett.) (Hymenoptera, Eulophidae): Observations on its occurrence and ultrastructure. *Canadian Journal of Zoology* 48: 959-964.
- Carlquist, S. (1969).—Studies in Stylidiaceae: new taxa, field observations, evolutionary tendencies. *Aliso* 7: 13-64.
- Churchill, D. (1961).—“The tertiary and quaternary vegetation and climate in relation to the living flora in south Western Australia.” Ph.D. Thesis, University of Western Australia.
- Crocker, R. L. (1959).—Past climatic fluctuations and their influence upon Australian vegetation. *Monographiae Biologicae* 8: 283-90.
- Crocker, R. L., and J. G. Wood (1947).—Some historical influences on the development of the South Australian vegetation communities and their bearing on concepts and classification in ecology. *Transactions of the Royal Society of South Australia* 71: 91-136.
- Darlington, C. D. (1958).—“The Evolution of Genetic Systems”. Allen and Unwin, London.
- de Zulueta, J. (1965).—The Rickettsia *Wolbachia pipiensis* in *C. pipiens* and *C. fatigans*. *WHO/VG/125.65*: 69-70. (Mimeographed document).
- Dobrotworsky, N. V. (1955).—The *Culex pipiens* groups in South-Eastern Australia. IV. Cross-breeding experiments within the *Culex pipiens* group. *Proceedings of the Linnean Society of New South Wales* 80: 33-43.

- Ey, T. M. and B. A. Barlow (1972).—Distribution of chromosome races in the *Eremophila glabra* complex. *Search* 3: 337-8.
- Farrell, Pauline (1973).—Biosystematic studies on two ephemeral species of *Stylidium*. (*In preparation*).
- Ford, J. and Parker, S. A. (1973).—A second species of Wedgehill. *Emu*. (*In press*)
- George, R. W. (1969).—Natural distribution and speciation of marine animals. *Journal of the Royal Society of Western Australia* 52: 33-40.
- George, R. W. and Main, A. R. (1967).—The evolution of spiny lobsters (Palinuridae): A study of evolution in the marine environment. *Evolution* 21: 803-820.
- Green, J. W. (1964).—Discontinuous and presumed vicarious plant species in southern Australia. *Journal of the Royal Society of Western Australia* 47: 25-32.
- Hayman, D. L. (1960).—The distribution of the chromosome races of *Themeda australis* in southern Australia. *Australian Journal of Botany* 8: 58-68.
- Hertig, M. (1936).—The rickettsia, *Wolbachia pipiens* (Gen. et Sp.N.) and associated inclusions of the mosquito, *Culex pipiens*. *Parasitology* 28: 453-490.
- Hertig, M. and Wolbach, S. B. (1924).—Studies on rickettsia-like micro-organisms in insects. *Journal of Medical Research* 44: 329-374.
- Irving-Bell, R. and Paterson, H. E. (1973).—Intracellular symbionts and infertility in mosquitoes of the *Culex pipiens* complex. *Science* (*In press*).
- James, S. H. (1965).—Complex hybridity in *Isotoma petraea*. I. The occurrence of interchange heterozygosity, autogamy and a balanced lethal system. *Heredity* 20: 341-53.
- James, S. H. (1971).—Complex hybridity in *Isotoma petraea*. II. Components and operation of a possible evolutionary mechanism. *Heredity* 35: 53-78.
- James, S. H. (1973).—Chromosome numbers and cytoevolution in Stylidiaceae. (*In preparation*.)
- Jost, E. (1970).—Untersuchungen zur Inkompatibilität in *Culex pipiens* Komplex. *Wilhelm Roux Archiv für Entwicklungsmechanik der Organismen* 166: 173-188.
- Kalmus, H. (1941).—Physiology and ecology of cutical colour in insects. *Nature, London* 148: 428-431.
- Kerr, R. W. (1961).—Inheritance of DDT resistance involving the Y-chromosome in the housefly (*Musca domestica*). *Australian Journal of Biological Sciences* 14: 605-619.
- Laven, H. (1953).—Reziprok Unterschiedliche Kreuzbarkeit von Stechmücken (Culicidae), and ihre Deutung als plasmatische Vererbung. *Zeitschrift für Vererbungslehre* 85: 118-136.
- Laven, H. (1967).—Speciation and Evolution in *Culex pipiens*. In: Wright J. W. and Pal R.: "Genetics of Insect Vectors of Disease". Elsevier, Amsterdam.
- Lee, D. J., Clinton, K. J. and O'Gower, A. K. (1954).—The blood sources of some Australian mosquitoes. *Australian Journal of Biological Sciences* 7: 282-301.
- Levin, D. A. (1970).—Reinforcement of reproductive isolation: Plants versus Animals. *American Naturalist* 104 (940): 571-581.
- Lewis, K. R. and B. John (1963).—"Chromosome Marker". J. and H. Churchill Ltd., London.
- L'Heritier, P. (1970).—*Drosophila* viruses and their role as evolutionary factors. *Evolutionary Biology* 4: 185-207.
- Mackerras, I. M. (1962).—Speciation in Australian Tabanidae. In Leeper, G. W. (ed.) "The evolution of living organisms". Melbourne University Press, Melbourne.
- Main, A. R. (1970).—Ecology, Systematics and Evolution of Australian Frogs. *Advances in Ecological Research* 5: 37-86.
- Main, A. R., Lee, A. K. and Littlejohn, M. J. (1958).—Evolution in three genera of Australian frogs. *Evolution* 12: 224-233.
- Main, B. Y. (1962).—Adaptive responses and speciation in the spider genus *Aganippe* Cambridge. In Leeper, G. W. (ed.) "The evolution of living organisms". Melbourne University Press, Melbourne.
- Marshall, J. F. and Staley, J. (1937).—Some notes regarding the morphological and biological differentiation of *Culex pipiens* Linnaeus and *Culex molestus* Forskal (Diptera, Culicidae). *Proceedings of the Royal Entomological Society of London (A)* 12: 17-26.
- Mayr, E. (1942).—"Systematics and the origin of species". Columbia University Press, New York.
- Mayr, E. Editor (1957).—"The Species Problem". American Association for the Advancement of Science, Washington.
- Mayr, E. (1963).—"Animal species and their evolution". Columbia University Press, New York.
- McComb, J. A. (1966).—The sex forms of species in the flora of the south-west of Western Australia. *Australian Journal of Botany* 14: 303-16.
- McComb, J. A. (1968).—The occurrence of unisexuality and polyploidy in *Isotoma fluviatilis*. *Australian Journal of Botany* 16: 525-37.
- McComb, J. A. (1969).—The genetic basis of sexuality in *Isotoma fluviatilis*. *Australian Journal of Botany* 17: 515-26.
- Milani, R. (1964).—Citologia della mosca domestica *Musca domestica* L. *Quaderni di La Ricerca Scientifica* 25: 111-116.
- Mildbraed, J. (1908).—Stylidiaceae. In Engler, A. "Das Pflanzenreich" IV, 278. Engelmann, Leipzig.
- Moore, J. A. (1957).—An embryologist's view of the species concept. In Mayr, E. Edit. "The Species Problem". American Association for the Advancement of Science, Washington.
- Parsons, P. A. (1958).—Evolution of sex in flowering plants of South Australia. *Nature* 181: 1673-4.
- Peacock, W. J. (1962).—Chromosome races in *Goodenia bellidifolia* Sm. *Proceedings of the Linnean Society of New South Wales* 87: 388-97.
- Peacock, W. J. (1963).—Chromosome numbers and cytoevolution in the Goodeniaceae. *Proceedings of the Linnean Society of New South Wales* 88: 8-27.
- Randell, Barbara R. (1970).—Adaptations in the genetic system of Australian arid zone *Cassia* species (Leguminosae, Caeraplinioideae). *Australian Journal of Botany* 18: 77-97.
- Rai, K. S. (1967).—Techniques for the study of cytogenetics and genetics of vectors. In Wright, J. W. and Pal, R. "Genetics of Insect vectors of Disease". Elsevier, Amsterdam.
- Rubini, P. G. (1964).—Polimorfismo cromosomico in *Musca domestica* L. *Bollettino di Zoologica* 31: 679-694.
- Sanderson, K. E. (1971).—Genetic homology in the Enterobacteriaceae. *Advances in Genetics* 16: 35-51.
- Serventy, D. L. and Wittell, H. M. (1951).—"Handbook of the birds of Western Australia". 2nd Edition. Lamb Publications, Perth.
- Shield, J. W. (1956).—Population studies in the littoral at Rottnest Island. *Journal of the Royal Society of Western Australia* 42: 89.
- Smith-White, S. (1959).—Cytological evolution in the Australian flora. *Cold Spring Harbour Symposium in Quantitative Biology* 24: 273-89.
- Thomson, J. A. (1969).—The interpretation of puff patterns in polytene chromosomes. *Currents in Modern Biology* 2: 333-338.
- Wagoner, D. E. (1969).—Presence of male determining factors found in three autosomes in the housefly, *Musca domestica*. *Nature, London* 223: 187-188.
- Yen, J. H. and Barr, A. R. (1971).—New hypothesis of the cause of cytoplasmic incompatibility in *Culex pipiens* L. *Nature, London* 232: 657-658.